THE TAXONOMY OF *ENTEROMORPHA* LINK, 1820 (CHLOROPHYCEAE) IN THE NETHERLANDS

III. The sections Flexuosae and Clathratae and an addition to the section Proliferae

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ABSTRACT. – On the basis of 202 living samples from 36 different stations, six *Enteromorpha* species were distinguished and described for the Netherlands coasts within the sections *Proliferae*, *Flexuosae* (Bliding's «Flexuosa Group», here including *E. ralfsii*) and *Clathratae* (Bliding's «Clathrata Group»). *E. linza* (Linnaeus) J. G. Agardh was added to the section *Proliferae*. *E. linziformis* Bliding, *E. pilifera* Kuetzing, *E. flexuosa* (Wulfen ex Roth) J. G. Agardh, and *E. ralfsii* Harvey were ranged in the section *Flexuosae*, and *E. clathrata* (Roth) Greville in the section *Clathratae*. Unialgal cultures were isolated from part of the samples in order to test the validity of the taxonomic criteria and to test the growth responses to varying salinities. The macroscopic morphology of the plants appeared to present the most distinctive differences between the species within the sections *Proliferae* and *Flexuosae*. The morphology of the basal parts and the morphology and distribution of filiform branchlets, if present, offered, additional criteria, whilst cell sizes and cell arrangements showed some, mostly minor differences. Diversity in the species of the sections *Proliferae*, *Flexuosae* and *Clathratae* in the Netherlands agrees well with the diversity recognized until now. *E. linziformis*, *E. pilifera*, *E. ralfsii* and *E. clathrata* are euryhaline species occurring in euhaline to mesohaline waters. *E. pilifera* and *E. flexuosa* grow even in oligohaline waters. *E. linza* consists of moderately euryhaline and widely euryhaline populations. The moderately euryhaline *E. linza* cultures only grew well in salinities ranging from 25-75 ‰ S. The widely euryhaline *E. linza* cultures and cultures of *E. linziformis* and *E. ralfsii* grew well in salinities ranging from 4-34 ‰ S. *E. pilifera* and *E. clathrata* grew well in 1,5-34 ‰ S, and *E. flexuosa* even in 0,5-34 ‰ S. In the discussion a key is presented to the four sections of *Enteromorpha* occurring in the Netherlands, (sections *Enteromorpha*, *Proliferae*, *Flexuosae*, *Clathratae*). These sections are distinguished on the basis of microscopic characters (arrangement and size of cells; number of pyrenoids per cell; position of chloroplasts in cells).

KEY WORDS : Chlorophyceae *Enteromorpha*, taxonomy, floristics, Netherlands coasts, morphology, reproduction, ecology, cultivation.

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INTRODUCTION

The present study completes a series of four papers on the taxonomy of Ulvales in the Netherlands. BLIDING's (1963, 1968) revisions of European Ulvales have led to the distinction of many more species (and subspecific taxa) in *Enteromorpha* and *Ulva* for European shores than previously recognized. BLIDING's revisions are based on living samples collected from widely distant points along the European coasts, and the number of samples studied per taxon is therefore necessarily limited in relation to the vastness of these coasts.

The question behind the present and preceding studies is whether a much more intensive sampling strategy in a much more limited geographical area would either lead to the same taxonomic concepts as BLIDING's or would produce morphological intermediates thus permitting the distinction of fewer, but geno- as well as phenotypically polymorphic species, or would disclose on the contrary, an even greater diversity on a much more local scale and this in relation to the vast estuarine gradients typical for the Netherlands coasts.

The results of the preceding studies in this series of papers on the taxonomy of the Netherlands species of *Ulva* (KOEMAN & van den HOEK, 1981), *Enteromorpha*, section *Enteromorpha* (KOEMAN & van den HOEK, 1982 a) and *Enteromorpha*, section *Proliferae* (KOEMAN & van den HOEK 1982 b), respectively, largely confirm BLIDING's taxonomic concepts, but revealed an even greater diversity than found by BLIDING. Moreover, the number of species inhabiting the Netherlands coasts appeared to be much greater than previously thought. The present paper reports the results of our researches on the taxonomy of *Enteromorpha linza*, which species is added to the section *Proliferae*; on *Enteromorpha*, section *Flexuosae*; and on the section *Clathratae* with only one species found in the Netherlands : *E. clathrata*. In the discussion, a key is presented to the four sections of *Enteromorpha* here recognized. As in the previous papers, we adopted as much as possible BLIDING's (1963) nomenclature.

MATERIAL AND METHODS

Material (126 living samples in *E. linza*, 65 in the section *Flexuosae* and 11 in the section *Clathratae* on a total of 676 samples in the genus *Enteromorpha*) was collected in the period from February 1975 through October 1977 from the stations indicated in Fig. 1, and described in Table I of KOEMAN and van den HOEK (1982 a). For particulars of sampling and description of natural material, see KOEMAN and van den HOEK (1981).

In addition, the morphology of about 7 days old cultured germlings was studied as well as the morphology of 30 days old plants cultured in media with the following salinities : 0.5 ‰ S (medium 1); 1.5 ‰ S (medium 2); 4 ‰ S (medium 3); 9 ‰ S (medium 4); 17 ‰ S (medium 5); 25 ‰ S (medium 6); 34 ‰ S (medium 7); and in some cases the hypersaline media 50 ‰ S (medium 8), and 75 ‰ S (medium 9). For a more complete treatment of the fig 1

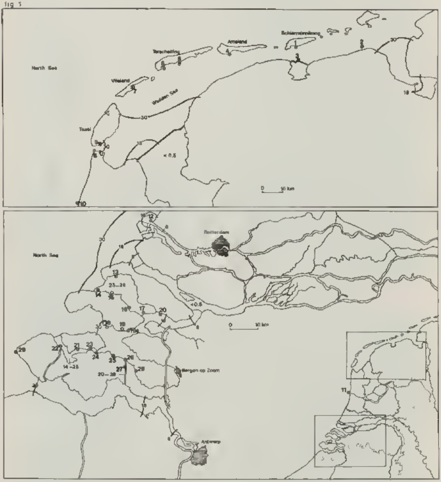


Fig. 1. — Map of the Netherlands showing stations and approximate isohalines in tidal waters and salinity ranges (‰ S) in nontidal waters. The investigated waters were divided into the following salinity sections : 1. euhalinicum (between the 32 and 30 ‰ S isohalines); 2. polyhalinicum (between the 30 and 18 ‰ S isohalines); 3. mesohalinicum (between the 18 and 5 ‰ S isohalines); and 4. the oligohalinicum (between 5 and 0.5 ‰ S isohalines). Moreover, some stagnant oligohaline to freshwater ditches were sampled (stations nrs : 2b, 3a, 4a, 8a, 10a, 16a, 18a, 18b, 26b).
Actually the tidal waters are subject to vast semidiurnal salinity fluctuations and fluctuations depending on river discharge, whereas the brackish man-made lakes show much less pronounced and yearly rather than dayly salinity fluctuations. Lake Grevelingen (stations 13 17) and Lake Veere (stations 21-24) used to be tidal estuaries, but were enclosed by dams and transformed into saline lakes in 1961 and 1971, respectively (for references see KOEMAN & van den HOEK, 1981).

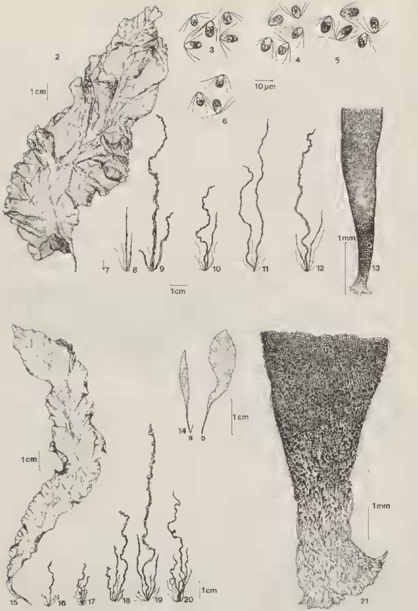


Fig. 2-21. — *E. linza*, 4-flagellate type. Fig. 2. plant no. 577. Figs 3, 4, 5, 6. 4-flagellate zoospores. Figs 7, 8, 9, 10, 11, 12. 30 days old cultures, same material as Fig. 2, Fig. 7 in 9 ‰ S medium, Fig. 8 in 17 ‰ S medium, Fig. 9 in 25 ‰ S medium, Fig. 10 in 34 ‰ S medium, Fig. 11 in 50 ‰ S medium, Fig. 12 in 75 ‰ S medium. Fig. 13. basis of plant no. 368. Fig. 14. young plants from nature; a, b, plants no. 85a and 85b respectively. Fig. 15. plant no. 368. Fig. 16, 17, 18, 19, 20. 30 days old cultures, same material as Fig. 15, Fig. 16 in 9 ‰ S medium, Fig. 17 in 17 ‰ S medium, Fig. 18 in 25 ‰ S medium, Fig. 19 in 34 ‰ S medium, Fig. 20 in 50 ‰ S medium. Fig. 21. basis of plant no. 577.

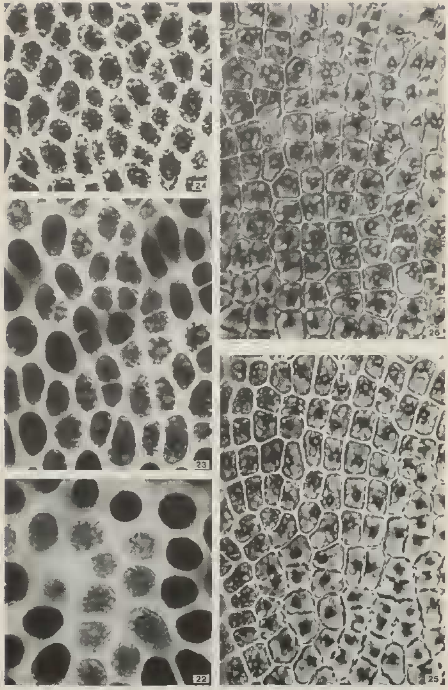


Fig. 22-26. – *E. linza*, 4-flagellate type, cells in surface view, same material as Fig. 2. Fig. 22. lower basal region, lower zone. Fig. 23. lower basal region, upper zone. Fig. 24. upper basal region. Fig. 25. middle region. Fig. 26. apical region.

methods used, see KOEMAN & van den HOEK (1981); for a description of the sampling stations, and criteria used for the distinction of species in *Enteromorpha*, see KOEMAN & van den KOEK (1982 a).

SECTION *PROLIFERAE* KOEMAN & van den HOEK (1982 b)

— ***E. LINZA*** **(Linnaeus) J.G. Agardh**

- Description (Figs 2-51)

Morphology (Figs 2, 7-21, 27, 29, 34-46)

Thalli strap-shaped, oblong, oblanceolate or irregular in outline, smooth, with undulating to ruffled, in mesohaline environments often entire margins; the two layers adnate and with hollow margins; rigid or lubricous. Plants unbranched or seldom with one or two broad branches in the upper basal part of the main frond. Medium green in euhaline environments to yellowish or light green in polyhaline to mesohaline environments. The basal parts of the thalli gradually narrowed, towards the base, into the firm (in large plants) to slender (in small plants) stipe, with a stout disciform holdfast, from which new thalli may arise. Plants up to 70 cm high and 15 cm broad, but mostly much smaller.

Anatomy, lower basal region (Figs 13, 21-23, 46-48)

In surface view, the stipe shows large dark and lighter coloured rhizoidal cells, which are interspersed by variously but mostly lighter coloured vegetative cells with which they form short undulating or curved cell rows. The vegetative cells may be also arranged without any order among the bigger rounded rhizoidal cells. Cell walls 2-9 μm thick. Chloroplast parietal, its structure sometimes obscured by large starch grains. In rhizoidal cells the chloroplasts mostly fill a large part of the rhizoids, which are thus quite conspicuous. In surface view the darker part just above the stipe shows many dark coloured rhizoidal and vegetative cells, which are more closely packed and mostly bigger than in the lower lighter coloured part of this region.

Anatomy, upper basal region (Figs 24, 49)

Cells in the upper basal region irregularly polygonal with 4-6 rounded corners, or elliptic to round, showing mostly slightly unequal divisions, unordered in full grown plants, or arranged in short to long undulating cell rows. Cell walls of full-grown plants characteristically thick : 4-8 μm, in younger plants 1-3 μm. The central thicker part of the parietal chloroplast, containing the mostly single pyrenoid, totally covering the outer cell wall, with thick arms descending along the anticlinal cell walls. The chloroplast structure is often obscured by numerous large starch grains. Pyrenoids 1; 2 in less than 20 % of the cells, 4-5 μm in diameter, round or elliptic.

Anatomy, middle and apical region (Figs 25, 26, 50, 51)

Cells in the middle and apical region characteristically quadrangular to rectangular, but often also irregularly polygonal in large areas of these regions, showing mostly equal divisions, arranged in short to long longitudinal and transverse cell rows, or rows with oblique orientation, often areas are interspersed in which order is much less clear. Cell walls in the middle region 1-4 μm, in the apical region 1-5 μm thick. The central thicker part of the chloroplast containing the pyrenoid(s) completely covering the outer cell wall, or tilted towards any anticlinal cell wall and having a more or less cap-like appearance in surface view, with rather thin descending arms. Pyrenoids 1 per cell, 2 in less than 20 % of the cells, 3-5 μm in diameter, round or elliptic.

Reproductive cells (Fig. 3-6, 28, 30-32)

In the collected material plants occurred which produced 4-flagellate zoids, and other plants which produced 2-flagellate zoids. Although simultaneous sporulation seldom occurred, 2-flagellate zoids from different plants were mixed in a few experiments, but no copulations were observed so that they are considered as asexual zoospores. Mostly they were positively phototactic, in some cases negatively phototactic, and in one case they showed no phototaxis.

Measurements based on 126 plants (in μm)

axis, cells in surface view :	
lower basal region, lower zone	(17-)22(-28) x (11-)13(-17)
lower basal region, upper zone	(14-)18(-25) x (9-)12(-14)
upper basal region	(11-)13(-16) x (8-)10(-11)
middle region	(11-)14(-16) x (8-)10(-11)
apical region	(12-)15(-18) x (9-)11(-13)
– 4-flagellate zoospores	(6.5-)8(- 9) x (5-) 6(- 7)
– 2-flagellate zoospores	(5.5-)6.5(-7.5) x (3.5-)4(-4.5)

Morphology of germlings and young fronds (Fig. 33)

Zoospores germinate by forming a rhizoid, immediately after that a strongly growing upright monoseriate filament. Mostly the rhizoidal part is well developed and contains many long branched rhizoids. In a later stage the filaments grow into hollow cylinders, which become compressed when a few cm high. More filaments may sprout from some spherical rhizoidal cells.

- Ecology and distribution

E. linza has been collected from 26 stations (see Table 1 and Fig. 1).

TABLE 1. — Specimens investigated
(for locality numbers see Table 1 in KOEMAN & van den HOEK, 1982a)

1 (II, '75, plants no. 32, 33; VII, '75, plants no. 48, 51, 52); 1c (V, '75, plants no. 19, 24); 2 (VIII, '75, plants no. 60, 63); 3 (IV, '75, plants no. 5, 6, 12); 4 (VI, '76, plants no. 546, 549); 4b (VI, '76, plant no. 560); 5 (III, '76, plants no. 243, 244, 245; V, '76, plants no. 463, 464, 465, 466, 467, 474, 475, 476; VI, '76, plants no. 536, 537, 538, 539, 545); 5a (V, '76, plants no. 488, 489); 6 (VI, '75, plants no. 85, 86 : III, '76, plants no. 275, 277); 6b (VI, '75, plants no. 160, 163, 164; III, '76, plant no. 281; VI, '76, plants no. 429a, 430, 431, 432, 529, 530); 7 (III, '76, plants no. 221, 222, 225, 226; V, '76, plants no. 433, 434, 435, 437, 438, 439, 440, 447, 448; VI, '76, plants no. 491, 492, 493, 495, 496, 497, 503); 7b (VI, '76, plants no. 518, 519, 520, 521, 523, 524); 10 (VI, '75, plants no. 189, 190, 191,

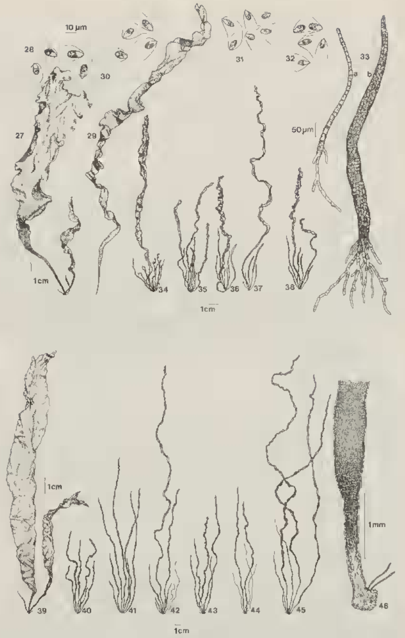
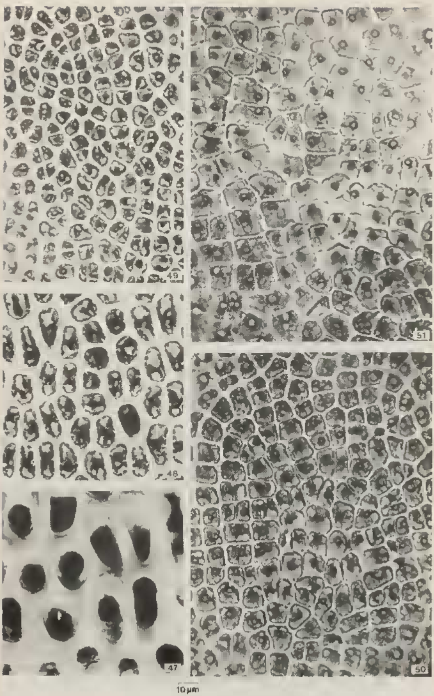


Fig. 27-46. – *E. linza*, 2-flagellate type. Figs 27, 29. plants with zoids, plants no. 243 and 345 respectively. Figs 28, 30, 31, 32. 2-flagellate zoids. Fig. 33. germlings, a after 5 days, b after 7 days. Figs 34, 35, 36, 37, 38. 30 days old cultures, same material as Fig. 29, Fig. 34 in 4 ‰ S medium, Fig. 35 in 9 ‰ S medium, Fig. 36 in 17 ‰ S medium, Fig. 37 in 25 ‰ S medium, Fig. 38 in 34 ‰ S medium. Fig. 39. plant no. 491. Figs 40, 41, 42, 43, 44, 45. 30 days old cultures, same material as Fig. 39, Fig. 40 in 1.5 ‰ S medium, Fig. 41 in 4 ‰ S medium, Fig. 42 in 9 ‰ S medium, Fig. 43 in 17 ‰ S medium, Fig. 44 in 25 ‰ S medium, Fig. 45 in 34 ‰ S medium. Fig. 46. basis of plant 491.



Figs 47-51. — *E. linza*, 2-flagellate type, cells in surface view, same material as Fig. 39. Fig. 47. lower basal region, lower zone. Fig. 48. lower basal region upper zone. Fig. 49. upper basal region. Fig. 50. middle region. Fig. 51. apical region.

192); 14 (IV, '76, plants no. 385, 389, 390, 392); 16 (IV, '76, plants no. 421a, 422a, 423a); 19 (IV, '76, plants no. 414, 415, 420a); 21 (VIII, '76, plant no. 588, 589); 22 (IV, '76, plants no. 323, 325, 326, 330); 22a (IV, '76, plants no 317, 320, 321); 23 (IV, '76, plants no. 297, 298, 299, 300, 301, 307, 311, 312, 314, 315, 316); 24 (IV, '76, plants no. 295, 296; VIII, '76, plants no. 564, 565, 566, 567); 26 (IV, '76, plants no. 357, 359); 26a (VIII, '76, plant no. 577); 27 (IV, '76, plants no. 398, 424; VIII, '76, plant no. 593); 28 (IV, '76, plants no. 366, 367, 368, 371); 29 (IV, '76, plants no. 337, 345, 428).

Four of these localities were lower littoral and upper sublittoral zones on sea-dikes and harbour moles exposed to strong wave action, seven were more sheltered, and include oysterponds. Four stations were low littoral sandy mudflats, where the species was often found abundantly growing attached to stones, wooden poles and shells in shallow tide pools and gullies. In high littoral stations the species was only found twice. Finally it was encountered in nine wave exposed localities in the polyhaline man-made lakes in the S.W. Netherlands. It was never found growing in oligo-to mesohaline ditches and canals.

2-flagellate and 4-flagellate clones of *E. linza* showed different responses to varying salinities in cultures. 2-flagellate clones in general gave good growth of germlings and young fronds in media with salinities ranging from 34-4 ‰; 4-flagellate clones, however, only in media with salinities ranging from 50-25 ‰ S. This accords well with the distribution of the two types of plants; the 2-flagellate type was mainly found in polyhaline environments, while the 4-flagellate type occurred in euhaline to polyhaline environments.

- Morphological and anatomical characters in cultures (Figs 7-12, 16-20, 34-38, 40-45)

The important morphological and anatomical characters were retained in cultures. However, cultured plants were much narrower. Most cells in the middle and apical region contained one large pyrenoid per cell, and the chloroplasts were situated more or less centrally against the outer cell wall. Cells in the broadest parts of the thalli were arranged in longitudinal and transverse rows, in narrower parts only in longitudinal rows. Plants cultured in low salinity media had larger cells than those in high salinity media (Tables 2-5).

TABLE 2 (cells dimensions in µm)

wild material of *E. linza* 577	medium	in culture
upper basal region (12-)15(-17) x (10-)11(-13)	6	(16-)20(-25) x (15-)17(-18)
middle region (12-)14(-16) x (8-) 9(-10)	6	(10-)12(-15) x (9-)10(-12)
apical region (12-)15(17) x (9-)10(-12)	6	(13-)18(-22) x (10-)11(-12)

TABLE 3 (cell dimensions in µm)

wild material of *E. linza* 546	medium	in culture
upper basal region	6	(20-)22(-24) x (13-)14(-14)
(12-)14(-15) x (8-) 9(-11)	3	(17-)20(-23) x (13-)15(-17)
middle region	6	(10-)15(-20) x (9-)11(-12)
(13-)15(-18) x (10-)12(-13)	4	(17-)19(-20) x (13-)14(-16)
	3	(22-)23(-27) x (15-)18(-22)
apical region	3	(13-)16(-20) x (12-)13(-13)
(13-)15(-17) x (10-)11(-13)		

TABLE 4 (cell dimensions in µm)

wild material of *E. linza* 345	medium	in culture
upper basal region	7	(12-)14(-15) x (9-)11(-13)
(14-)17(-19) x (10-)12(-13)	6	(24-)28(-33) x (10-)13(-16)
	5	(10-)14(-17) x (9-)11(-13)
	4	(13-)17(-21) x (9-)12(-14)
	3	(16-)20(-25) x (7-)10(-13)
middle region	7	(9-)12(-14) x (6-) 8(- 9)
(11-)14(-16) x (8-)10(-11)	6	(11-)15(-20) x (9-)11(-14)
	5	(11-)15(-19) x (8-)10(-13)
	4	(14-)16(-19) x (9-)11(-14)
	3	(19-)22(-26) x (13-)17(-22)
apical region	7	(10-)12(-14) x (7-) 9(-11)
(14-)16(-18) x (11-)12(-14)	6	(10-)16(-22) x (10-)12(-14)
	5	(10-)12(-15) x (8-)10(-12)
	4	(13-)17(-21) x (10-)12(-13)
	3	(18-)21(-25) x (14-)16(-19)

TABLE 5 (cell dimensions in µm)

wild material of *E. linza* 491	medium	in culture
upper basal region	7	(8-)10(-12) x (7-) 9(-11)
(14-)18(-21) x (- 9)10(-12)	6	(11-)14(-17) x (8-)10(-13)
	5	(11-)14(-18) x (9-)11(-13)
	4	(15-)17(-19) x (11-)13(-16)
	3	(16-)20(-23) x (11-)13(-15)
	2	(16-)23(-31) x (11-)14(-18)
middle region	7	(11-)13(-16) x (8-)10(-13)
(10-)13(-15) x (7-) 9(-11)	6	(12-)14(-17) x (8-)10(12)
	5	(12-)15(-19) x (9-)11(-14)
	4	(14-)17(-20) x (10-)11(-13)
	3	(16-)21(-26) x (12-)14(-17)
	2	(19-)24(28) x (11-)15(-19)
apical region	7	(15-)16(18) x (9-)11(-14)
(14-)16(-18) x (10-)13(-15)	6	(12-)14(-16) x (9-)11(-13)
	5	(12-)15(-18) x (10-)12(-14)
	4	(15-)17(-19) x (10-)12(-13)
	3	(15-)20(-24) x (11-)13(-16)
	2	(19-)25(-32) x (12-)15(-19)

SECTION *FLEXUOSAE* NOV. SECT.

Lectotype of the genus *Enteromorpha* Link, 1820 (nom. cons.) is *E. intestinalis* (L.) Link (SILVA, 1952, p. 294; PAPENFUSS, 1962, p. 314). Type species of the section *Flexuosae* is *E. flexuosa* (Wulfen ex Roth) J. G. Agardh (cf. BLIDING, 1963, p. 73). The section *Flexuosae* largely agrees with BLIDING's (1963, p. 73) «Flexuosa Group». However, *E. ralfsii* Harvey is here included in this section. BLIDING places *E. ralfsii* in the «Torta Group».

Cells in the basal region varying from about 15 x 9 to 30 x 20 µm. Cells in middle region varying from about 12x9 to 19x14 µm. Cells in apical and middle region showing mostly equal divisions, and being arranged in longitudinal and sometimes transverse rows. The parietal chloroplast containing the mostly 1-5 pyrenoids usually situated centrally against the peripheral cell wall, or slightly tilted towards any anticlinal cell wall, with rather thin lobes descending along some anticlinal cell walls. Thallus filiform to linear, the broader thalli oblong in outline, mostly compressed, the two layers loosely adnate, leaving a hollow margin, or tubular; unbranched or with main branches (having the same form as the axis) and branchlets concentrated towards the basal region, or along the whole axis.

Latin diagnosis :

Cellulae regionis basalis magnitudine c. 15 x 9 usque ad 30 x 20 µm, cellulae regionis medianae magnitudine c. 12 x 9 usque ad 19 x 14 µm. Regionis apicalis et medianae cellulae divisionibus plerumque aequalibus in seriebus longitudinalibus et interdum transversalibus. Chloroplastus plerumque integumentum cellulare externum tegens 1-5 pyrenoidibus. Thallus filiformis - linearis - oblongus; plerumque complanatus cellularum duobus stratis laxe adnatis marginibus cavis, sive tubulosus; simplex vel, ramis forma axium et ramulis praecipue in axis regione basali seu extendentibus secus axes totas.

Identification of species in the section *Flexuosae*

Identification of the four species of *Enteromorpha* in the section *Flexuosae* is facilitated by Table 6 which permits the comparison of combinations of characters.

— *E. LINZIFORMIS* Bliding

E. flexuosa subsp. *linziformis* (Bliding) Bliding, 1963, p. 87.

- Description (Figs 52-85)

Morphology (Figs 52, 54, 56, 58, 60, 79)

Thalli strapshaped, oblong or linear in outline, smooth, with entire margins, the two layers compressed and loosely adnate with hollow margins, lubricous, light to medium green, at least with a few microscopic branchlets near the base. Full grown plants from open populations often have a few branches concentrated in the basal part of the frond, with about the same length as but narrower than the main axis. Apex of main axis obtuse, mostly open. Basis attenuate, stipe long, slender, with a small disciform holdfast. Length up to 80 cm and width up to 4 cm, but mostly not more than 30 cm long and 2 cm broad.

Anatomy, lower basal region (Figs 79, 81, 82)

In surface view, the stipe shows elongate rhizoidal cells with rounded corners. In young plants they cannot be distinguished from normal vegetative cells. In older plants only in the lowest part of this region rhizoidal outgrowths of these cells are visable. Cells are in general well ordered in longitudinal rows, in young plants even in short transverse rows. Cell walls 2-8 µm thick, thickest in the upper part of this region. Chloroplast parietal against the peripheral cell wall, with thin smooth lobes descending along the anticlinal cell walls, seldom obscured by starch grains, containing 3-8 pyrenoids per cell.

Anatomy, upper basal region (Fig. 83)

Cells in the upper basal region irregularly polygonal with 3-5 rounded corners, showing mostly unequal divisions, mostly well ordered in long longitudinal rows, or partly in short curved rows. The longitudinal cell rows are characteristically separated from each other by thicker cell walls. Cell walls 1-4 µm thick. Chloroplast parietal against the peripheral cell wall, with some thin lobes descending along the anticlinal cell walls. The chloroplast structure is seldom obscured by starch grains. Pyrenoids 2-5 per cell, 1 in some small just divided cells, 2-4 µm in diameter, round or elliptic.

Anatomy, middle and apical region (Figs 84, 85)

Cells in the middle and apical region irregularly polygonal with 4-6 corners, showing equal to slightly unequal divisions, arranged in 4-8 celled rows with oblique or longitudinal orientation often separated from each other by slightly thicker cell walls. Cell walls in the middle region 0.5-2 µm, in the apical region up to 4 µm thick. The parietal chloroplast sometimes slightly tilted towards any anticlinal cell wall or predominantly towards the apically oriented one, with rather thin lobes descending along the anticlinal cell walls. The chloroplast structure is seldom obscured by starch grains. Pyrenoids 2-5 per cell, 1 in very small just divided cells, round or elliptic.

Anatomy, tips of short filiform branchlets (Fig. 80)

The monoseriate apex of young branches is 1-3(8) cells long and frequently ends in one tip cell which is slightly bigger than the other cells just below. Except the most basal cells the cells of filiform branchlets are smaller than normal thallus cells.

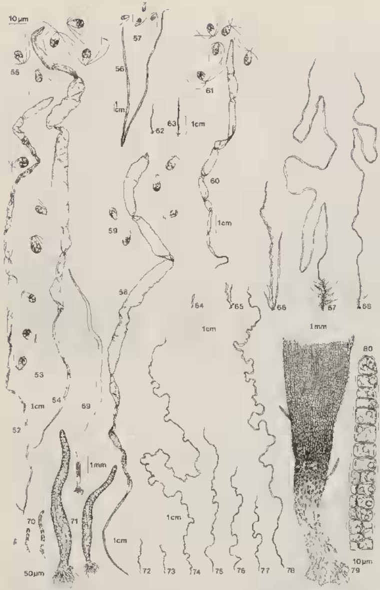
Reproductive cells (Figs 53, 55, 57, 59, 61)

In the collected material mainly plants occurred which produced 4-flagellate zoids; however, some plants produced 2-flagellate zoids; the offspring of some of these plants produced zoids of the same kind again. They were always positively phototactic and able to germinate soon.

TABLE 6 : Identification table of section *Flexuosae*

E. linziformis	*E. pilifera*	*E. flexuosa*	*E. ralfsii*
Thalli strap-shaped, with only few mostly microscopic branchlets near the base, margins entire (the two layers loosely adnate).	Thalli strap-shaped to filiform, in general densely branched, tubular or compressed, the two layers not adnate, wrinkled in broad parts.	Thalli strap-shaped to filiform, in general densely branched, compressed, in broad parts the two layers adnate with hollow margins, smooth (not wrinkled).	Thalli filiform, unbranched.
Central cavity at least 25 μm in diameter, in small branches.	Central cavity at least 25 μm in diameter, in small branches.	Central cavity at least 25 μm in diameter, in small branches.	Central cavity 8-12 μm in diameter.
Monoseriate apex of filiform branchlets 1-3(8) cells long, tip cell slightly bigger than the cells just below.	Monoseriate apex of filiform branchlets 4-20 cells long, tip cell 1-2 times as big as the other cells	Monoseriate apex of filiform branchlets 1-6 cells long, tip cell up to twice as big as the other cells.	Multiseriate apex without dominant tip cell.
Axis gradually narrowed into a long, slender stipe.	Axis gradually narrowed into a very long, slender stipe.	Axis gradually narrowed into a fragile stipe.	In nature always without stipe.
Cells in basal regions arranged in long undulating rows separated from each other by thicker cell walls, consisting of elongate dark coloured rhizoidal and lighter coloured vegetative cells. Cell walls 2-8 μm thick, 1-4 μm in the upper part of the region.	Cells in basal regions arranged in longitudinal and sometimes transverse rows consisting of dark coloured elongate rhizoidal cells and lighter coloured vegetative cells, which may be united in pairs in the upper part of the region. Cell walls 1-6 μm thick, thickest in the upper part of the region.	Cells in basal regions arranged in longitudinal and sometimes transverse rows consisting of dark coloured elongate rhizoidal cells and in the upper part of the region of lighter coloured elongate vegetative cells, often some cell rows are conspicuous by their narrower and longer cells. Cell walls 1-5 μm thick.	Cells in all regions with the same features, see below.

Cells in middle and apical regions showing equal to nearly equal divisions, irregularly polygonal with 4-6 corners, arranged in 4-8 celled rows with oblique or longitudinal orientation, often separated from each other by thicker cell walls. Cell walls 0.5-4 µm thick, thickest in the apical region.	Cells in broad middle and apical regions showing equal to unequal divisions, irregularly polygonal with 4-6 often rounded corners, very variable in size, mostly arranged in 2-8 celled unordered groups and which are separated from each other by thick cell walls, up to 10 µm thick. In narrow parts of these regions, cells are mostly well ordered in longitudinal rows. Cell walls 0.5-2 µm thick.	Cells in middle and apical region showing equal divisions, rectangular, quadrangular or irregularly polygonal often with rounded corners, arranged in longitudinal and short transverse rows. In the middle region some cell rows consist of narrower and longer cells. Cell walls 0.5-2 µm thick, the longitudinal ones thickest.	Cells showing equal divisions, mostly rectangular or quadrangular, arranged in long longitudinal rows. Cell walls 0.5-2 µm thick. Sometimes 2-4 celled rows are separated from each other by a thicker transverse cell wall.
Cells in middle region (13-) 15 (-18) x (9-) 11 (-12) µm.	Cells in middle region (12-) 16 (-19) x (11-) 12 (-14) µm.	Cells in middle region (11-)14(-16) x (8-)9(-11) µm.	Cells (15-)18(-21) x (9-) 11(-12) µm.
Pyrenoids (1-)2-5 per cell, 2-4 µm, round or elliptic.	Pyrenoids 1-6 per cell, 2-4µm, round.	Pyrenoids 1-5 per cell, 2-5 µm, round.	Pyrenoids 2-6 per cell, 2-4 µm, round or elliptic.
Reproduction only by 4-flagellate, exceptionnally 2-flagellate zoids (probably asexual zoospores).	Reproduction by either 2-flagellate ♂ and ♀ gametes, or by 4-flagellate zoospores (alternation of gametophyte and sporophyte generations).	Reproduction by either 2-flagellate ♂ and ♀ gametes, or by 4-flagellate zoospores (alternation of gametophyte and sporophyte generations).	Reproduction only by 4-flagellate zoids (probably asexual zoospores).



Figs 52-80. – *E. linziformis.* Figs 52, 54, 56, 58, 60. plants with zoids. Figs 52, 54, 60. sporophytes, plants no. 587, 589, 586 respectively. Fig. 56. male gametophyte, plant no. 598. Fig. 58. female gametophyte, plant no. 590. Figs 53, 55, 61. zoospores, Fig. 57. male gametes. Fig. 59. female gametes. Figs 62, 63. 30 days old cultures, same material as Fig. 56, Fig. 62 in 25 ‰ S medium, Fig. 63 in 34 ‰ S medium. Figs 64, 65, 66, 67, 68. 30 days old cultures, same material as Fig. 52, Fig. 64 in 4 ‰ S medium, Fig. 65 in 9 ‰ S medium, Fig. 66 in 17 ‰ S medium, Fig. 67 in 25 ‰ S medium, Fig. 68 in 34 ‰ S medium. Fig. 69, 70, 71, germlings, same material as Fig. 58, Fig. 69 after 17 days, Fig. 70 after 5 days, Fig. 71 after 12 days. Fig. 72, 73, 74, 75, 76, 77, 78. 30 days old cultures, same material as Fig. 58, Fig. 72 in 0.5 ‰ S medium, Fig. 73 in 1.5 ‰ S medium, Fig. 74 in 4 ‰ S medium, Fig. 75 in 9 ‰ S medium, Fig. 76 in 17 ‰ S medium, Fig. 77 in 25 ‰ S medium, Fig. 78 in 34 ‰ S medium. Fig. 79. basis of plant 560. Fig. 80. tip of branchlet, same material as Fig. 56.

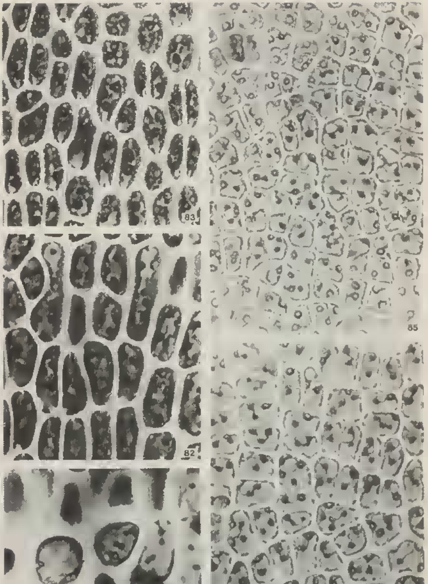


Fig. 81 85. — *E. linziformis*, cells in surface view, same material as Fig. 54. Fig. 81. lower basal region, lower zone. Fig. 82. lower basal region, upper zone. Fig. 83. upper basal region. Fig. 84. middle region. Fig. 85. apical region.

Measurements, based on 16 plants (in μm)

– axis, cells in surface view :	
lower basal region, lower zone	(20-)25(-29) x (12-)14(-16)
lowet basal region, upper zone	(16-)20(-25) x (9-)12(-14)
upper basal region	(13-)17(-20) x (9-)11(-13)
middle region	(13-)15(-18) x (9-)11(-12)
apical region	(12-)15(-18) x (9-)11(-13)
– branches, cells in surface view :	
basal region	(25-)29(-34) x (9-)11(-12)
middle region	(13-)16(-19) x (10-)11(-13)
apical tegion	(12-)15(-17) x (9-)10(-12)
– 2-flagellate zoids	(5.5-)6(-7) x (3.5-)4(-4.5)
– 4-flagellate zoids	(6-)7.5(-8.5) x (5-) 6(-7)

Morphology of germlings and young fronds (Figs 69-71)

Zoids germinate by forming a short rhizoid, and immediately after that a strongly growing upright uniseriate filament. The first formed rhizoidal cell divides into new cells which form more rhizoids. At a later stage these filaments grow into hollow cylinders which become compressed when grown large enough.

- Ecology and distribution

E. linziformis has been collected from 5 stations (see Table 7 and Fig. 1).

TABLE 7. — Specimens investigated
(for locality numbers see Table 1 in KOEMAN & van den HOEK, 1982a)

5 (V, '76, plants no. 472, 483); 6b (VI, '75, plants no. 165, 166, 167; VI, '76, plant no. 533); 7 (V, '76, plants no. 436, 442); 21 (VIII, '76, plants no. 584, 585, 586, 587, 589, 590); 23 (IV, '76, plants no. 308, 309).

Two of these localities were low littotal sandy mudflats where the species was growing submerged in gullies and tidal ponds. Two other localities were polyhaline man-made lakes in the S.W. Netherlands. One station was on a low littoral sheltered seadike. It was never found growing in wave exposed or high littoral places or in oligohaline environments. This accords with our cultures, which gave good growth in media with salinities ranging from 34-9 ‰ S. Some growth even occurted at 4-1.5 ‰ S.

- Morphological and anatomical characters in cultures (Figs 62-68, 72-78)

The important morphological and anatomical characters were retained in cultures; however the plants remained narrower, and branching was sometimes denser than in natural plants. The branches were always concentrated, as in the wild material, on the basal part of the stem. Most cells contained 2-3 pyrenoids per cell, the highest average number occurred at the lowest salinities tested. The parietal chlotoplast covered the outer cell wall, or was slightly tilted towards the apically oriented anticlinal cell wall. In contrast to wild material, the chloroplast structure was often obscured by numerous starch grains. At the higher salinities tested, cells tended to be smaller than in the wild material. In general the cells were well ordered in longitudinal rows and less so in transverse rows; in some parts of the largest plants short rows showed a diverse orientation (Table 8).

TABLE 8 (cell dimensions in μm)

wild material of *E. linziformis* 590	medium	in culture
upper basal region	7	(18-)24(-30) x (15-)18(-22)
(19-)24(-30 x (9-)12(-15)	6	(14-)18(-21) x (11-)15(-19)
	5	(14)17(-19) x (11-)12(-14)
	4	(17-)19(-22) x (14-)15(-16)
	3	(19-)21(-24) x (17-)19(-20)
	2	(21-)26(-32) x (18)22(-26)
middle region	7	(14-)17(-21) x (9-)12(-14)
(13-)16(-19) x (10-)12(-14)	6	(14-)17(-20) x (10-)13(-17)
	5	(12-)17(-21) x (11-)13(-15)
	4	(15-)17(-19) x (11-)13(-16)
	3	(20-)25(-29) x (16-)20(-23)
	2	(16-)20(-24) x (11-)14(-17)
apical region	5	(17-)19(-22) x (11-)15(-19)
(18-)20(-22) x (11-)13(-15)	4	(19-)22(-25) x (16-)19(-22)
	3	(20-)23(-25) x (14-)17(-19)
	2	(15-)19(-23) x (12-)14(-17)

– *E. PILIFERA* Kuetzing

E. flexuosa subsp. *pilifera* (Kuetz.) Bliding, 1963, p. 91.

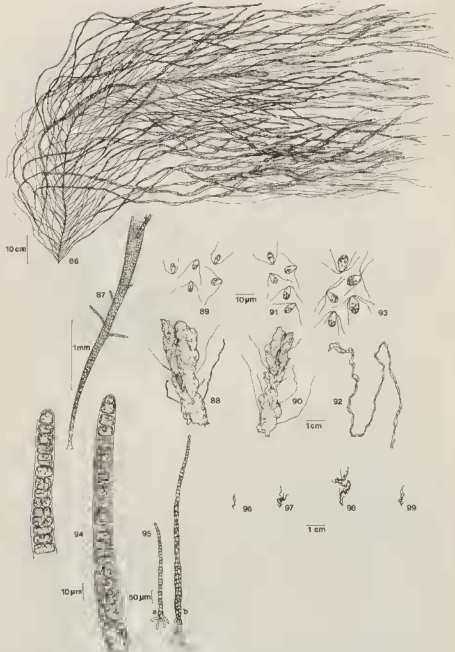
· Description (Figs 86-105)

Morphology (Figs 86-88, 90, 92)

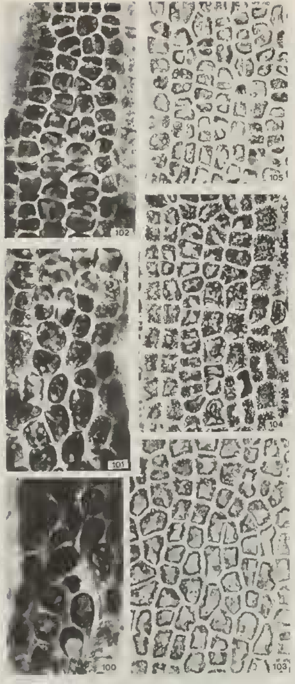
Thalli strap-shaped to filiform; tubular, or the two layers compressed but not adnate, wrinkled in broad parts, mostly very lubricous, light or yellowish green. Young plants sparsely branched, filiform mature plants densely branched along the whole main axis, with branches of the first and second order, or of the first order only. Axis gradually narrowed towards the base into a very long fragile stipe, with a small disciform holdfast, from which seldom new thalli arise. Main branches with extremely long filiform basal parts. Apices of axis and main branches of full grown plants obtuse, mostly open or damaged. Axis and main branches up to 2 m long and 3 cm broad, but often floating in dense masses of fragmented individuals.

Anatomy, lower basal region (Figs 87, 100, 101)

In surface view, the stipe shows dark coloured elongate rhizoidal cells which gradually merge into a zone of equally sized lighter coloured vegetative cells. In this part cells form longitudinal rows and sometimes even transverse rows, particularly in young individuals. Cell walls 1-6 μm thick. The parietal chloro-



Figs 86-99. – *E. pilifera.* Fig. 86. plant no. 75a. Fig. 87. basis of a 25 cm long plant. Figs 88, 90, 92. fragments of fertile plants, with zoids. Figs 89, 91, 93. male gametes, female gametes and zoospores respectively. Fig. 94. tips of branchlets. Fig. 95. germlings, a after 5 days, b after 10 days. Fig. 96, 97, 98, 99. 30 days old cultures, same material as Fig. 90, Fig. 96 in 0.5 ‰ S medium, Fig. 97 in 1.5 ‰ S medium, Fig. 98 in 9 ‰ S medium, Fig. 99 in 34 ‰ S medium.



Figs 100-105. — *E. pilifera*, cells in surface view, same material as Fig. 86. Fig. 100. lower basal region, lower zone. Fig. 101. lower basal region, upper zone. Fig. 102. upper basal region. Fig. 103. middle region. Fig. 104. apical region. Fig. 105. apical region of main branch.

plast covering the outer cell wall, sometimes tilted towards the apically oriented anticlinal cell wall. Pyrenoids 4-6 per cell, 2 in small cells. Descending arms thick, thin in young individuals. The chloroplast structure, however, is often obscured by numerous starch grains. The darker part just above the rhizoidal zone shows smaller sized cells, which may have thick cell walls and are arranged with less order in older plants.

Anatomy, upper basal region (Fig. 102)

Cells in the upper basal region irregularly polygonal or rectangular with 4-6 rounded corners, showing equal divisions, arranged in mostly distinct longitudinal rows, or in pairs, which are arranged in distinct longitudinal rows, sometimes even in short transverse rows. Cell walls 3-6 μm thick, in young individuals 1-4 μm. The chloroplast is mostly situated against the outer cell wall, consisting of a thin central part with relatively thick arms containing the pyrenoids, descending along the anticlinal cell walls. Sometimes the chloroplasts are tilted in cell pairs away from each other, or predominantly towards the apically oriented cell wall. The chloroplast structure is sometimes obscured by numerous starch grains. Pyrenoids 2-6 per cell, 2-4 μm in diameter.

Anatomy, middle and apical region (Figs 103-105)

Cells in the middle and apical region very variable in size, arrangement and form. In general, broad parts of these regions consist of small cells which are irregularly polygonal with 4-6 corners, or rounded, showing equal to unequal divisions. The cells are mostly arranged in 2-8 celled unorderly groups, which can be recognized by their common thick cell wall. Cell walls in such parts up to 10 μm thick. Narrower plant parts, particularly those of the long and slender main branches show cells which are irregularly polygonal to rectangular or quadrangular showing equal to slightly unequal divisions perpendicular to the frond's axis. Cells are here arranged in long longitudinal often undulating rows, in broader parts these rows become more and more disturbed by groups of cells which show less order. Cell walls in this region 0.5-2 μm thick. In the smaller celled parts of the fronds the parietal chloroplasts cover the outer cell wall, or are slightly tilted towards any anticlinal cell wall. Often the chloroplast structure is obscured by large starch grains. Pyrenoids 1-3 per cell, round. In the narrower parts with larger cells, the parietal chloroplasts cover the outer cell wall, or are slightly tilted towards the apically oriented anticlinal cell wall, with rather thin arms descending along the anticlinal cell walls; they often have a distinct uniform density. In this part the chloroplast structure is seldom obscured by starch grains. Pyrenoids 2-6 per cell, round.

Anatomy, tips of short filiform branchlets (Fig. 94)

In surface view, the monoseriate apex of young branchlets is 4-20 cells long. The tip-cell is 1-2 times as big as the cells just below, which in their turn are somewhat smaller than normal thallus cells of branching regions. Very young branchlets of 2-4 cells are clearly visible because of their dark chloroplasts and big cells.

Reproductive cells (Figs 89, 91, 93)

In nature plants are dioecious gametophytes, producing 2-flagellate gametes, the male ones slightly smaller and with smaller chloroplasts than the female ones; or sporophytes which produce big 4-flagellate zoospores. They were all positively phototactic and germinated very soon.

Measurements based on 8 plants (in µm)

– axis, cells in surface view :	
lower basal region, lower zone	(18-)24(-30) x (14-)17(-20)
lower basal region, upper zone	(18-)22(-25) x (13-)15(-17)
upper basal region	(15-)19(-22) x (12-)14(-16)
middle region	(12-)16(-19) x (11-)12(-14)
apical region	(9-)14(-19) x (7-)11(-15)
– branches, cell in surface view :	
basal region	(19-)23(-25) x (13-)15(-17)
middle region	(13-)17(-20) x (11-)12(-14)
apical region	(14-)17(-20) x (12-)13(-15)
– male gametes	(5-) 6(- 7) x (3.5-)4(-4.5)
– female gametes	(6-)6.5(-7.5) x (3.5-)4.5(-5.5)
– zoospores	(7.5-)9(-10.5) x (4.5-)5.5(-6)

Morphology of germlings and young fronds (Fig. 95)

Zoospores and fused as well as unfused gametes germinate by forming a rhizoid, this rhizoid at first grows very strongly, and may branch before an upright growing filament is formed. The growth of this filament is also very strong, while the rhizoidal system shows intense branching. From some spherical rhizoidal cells often more filaments are formed. In a later stage the filaments grow into hollow cylinders. The first formed frond, the main axis, may form branches along its whole length, or predominantly on the basal part.

- Ecology and distribution

E. pilifera has been collected from 3 stations (see Table 9 and Fig. 1).

TABLE 9. – Specimens investigated
(for locality numbers see Table 1 in KOEMAN & van den HOEK 1982a)

1b (VII, '75, plants no. 57, 58); 10a (VI, '75, plants no. 75a, 75b; VII, '75, plant no. 188); 26b (VI, '75, plants no. 73b, 74b, 74c).

Two of these localities were meso- to oligohaline stagnant waters. One station was a low littoral tidal pool on a sandy mudflat. It was never found growing in exposed places. This distribution suggests the species to be euryhaline. This agreed with our cultures, which gave some growth at all salinities tested. However, the species was difficult to maintain in culture.

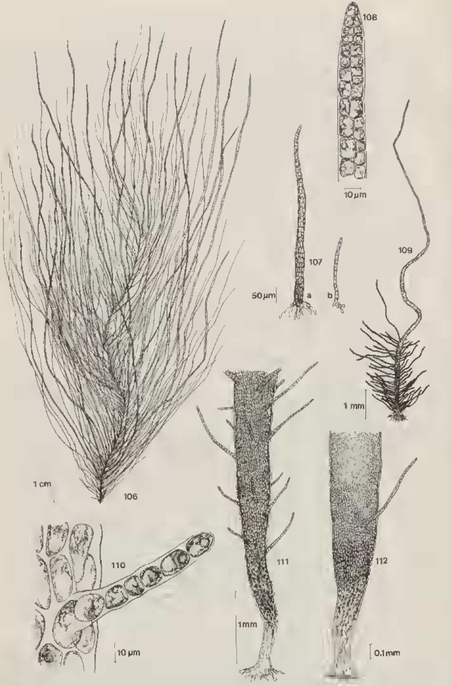


Fig. 106-112. — *E. flexuosa.* Fig. 106. plant no. 552. Fig. 107. germlings, a after 10 days, b after 5 days. Fig. 108. tip of branchlet. Fig. 109. germling. after 15 days. Fig. 110. monoseriate branchlet. Fig. 111, 112. bases of plants no. 552 and 470 respectively.

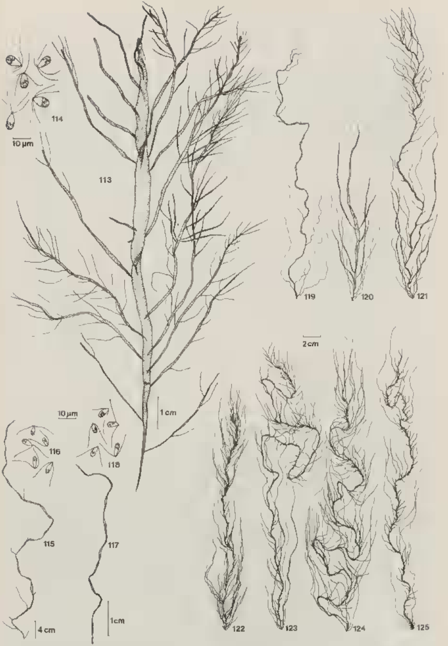


Fig. 113-125. – *E. flexuosa.* Fig. 113, 115, 117. plants with zoids, plants no. 418, 534 and 162, respectively. Fig. 114. zoospores. Fig. 116. male gametes. Fig. 118. female gametes. Fig. 119, 120, 121, 122, 123, 124, 125. 30 days old cultures, same material as Fig. 113, Fig. 119 in 0.5 ‰ S medium, Fig. 120 in 1.5 ‰ S medium, Fig. 121 in 4 ‰ S medium, Fig. 122 in 9 ‰ medium, Fig. 123 in 17 ‰ S medium, Fig. 124 in 25 ‰ S medium, Fig. 125 in 34 ‰ S medium.

- Morphological and anatomical characters in cultures (Figs 96-99)

Cultured plants never reached the size of plants from nature as, for unknown reasons, they did not grow well when a few cm high. Cultured plants were sparsely branched and very narrow, with typical branch-tips. Only at the lowest salinities tested did the cells contain 2-6 pyrenoids. At the higher salinities tested most cells contained 1-2 pyrenoids. The parietal chloroplasts were often tilted towards the laterally oriented anticlinal cell walls, especially at the higher salinities. Cells were on the whole not well ordered, unlike the material from nature. Plants cultured in low salinity media had bigger cells than those in high salinity media (Table 10).

TABLE 10 (cell dimensions in μm)

wild material of *E. pilifera* 57	medium	in culture
upper basal region (16-)18(-21) x (12-)14(-16)	1	(18-)22(-26) x (12-)16(-21)
middle region (16-)18(-21) x (11-)12(-14)	7	(14-)17(-20) x (10-)12(-14)
	4	(18-)20(-23) x (12-)15(-18)
	2	(12-)15(-17) x (9-)11(-13)
	1	(10-)13(-15) x (7-)10(-12)
apical region (13-)14(-16) x (9-)11(-12)	1	(14-)15(-16) x (10-)13(-15)

— *E. FLEXUOSA* (Wulfen ex Roth) J. G. Agardh

- Description (Figs 106-130)

Morphology (Figs 106, 111-113, 115, 117)

Thalli strapshaped to filiform, the two layers compressed, in broad parts the two layers adnate with hollow margins, otherwise hollow, smooth, with mostly lubricous texture, yellowish green to light green, branched, full grown plants seldom unbranched. Branched plants with branches of the first order along the whole main axis, or mainly concentrated in the basal region of the thallus. Densely branched plants often with second order branches along the main branches. Axis gradually narrowed towards the base into a fragile stipe, with a small disciform holdfast, from which new thalli may arise. Apices of axes, even the strapshaped ones, and main branches filiform to acute, if not damaged. Axis and main branches up to 60 cm high and 1 cm broad, but mostly not more than 40 cm long and 0.5 cm broad.

Anatomy, lower basal region (Figs 111, 112, 126, 127)

In surface view, the stipe shows dark coloured rounded, often elongate rhizoidal cells, whose rhizoids may grow through the central cavity as well as along the outer side of the stipe. Vegetative cells are absent or rare; they show nearly the same morphology as rhizoidal cells. In this part cells form longitudinal and often transverse rows. Cell walls 1-4 μm thick. The central thicker part of the chloroplast containing the pyrenoids mostly slightly tilted towards the apically oriented anticlinal cell wall, or situated centrally against the peripheral cell wall, often as a transverse band. Descending arms relatively thin, descending along the anticlinal cell walls. The chloroplast structure, however, is often obscured by numerous small or large starch grains. In surface view, the darker part just above the stipe shows many dark coloured vegetative as well as rhizoidal cells, which may be somewhat smaller than those of the zone below, but otherwise show the same features. 2-3 pyrenoids per cell, 1 in up to 50 % of the cells, 3-5 μm in diameter, round.

Anatomy, upper basal region (Fig. 128)

Cells in the upper basal region rounded or rectangular with rounded corners, showing nearly equal divisions, arranged in longitudinal rows, sometimes also in transverse rows. Often some longitudinal cell rows are conspicuous by their narrower and longer cells. Cell walls 1-5 μm thick. The central thicker part of the chloroplast containing the pyrenoids is situated centrally against the peripheral cell wall or is slightly tilted towards the apically oriented anticlinal cell wall; sometimes it forms a transverse band against the peripheral cell wall, with rather thin lobes descending mainly along the lateral anticlinal cell walls. Some small or large starch grains may occur. 2-5 pyrenoids per cell, 1 in up to 50 % of the cells, the lower numbers more frequent than the higher ones, 2-4 μm in diameter, round.

Anatomy, middle and apical region (Figs 129, 130)

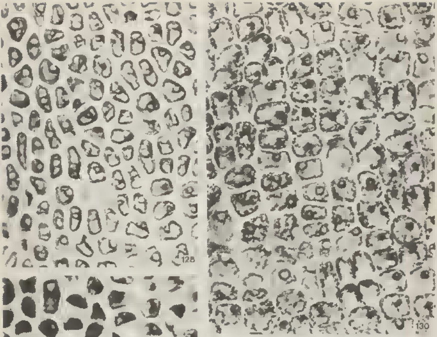
Cells in the middle and apical region rectangular, quadrangular or irregularly polygonal with or without rounded corners, showing equal divisions, arranged in longitudinal and short transverse rows, especially in broader parts of the thallus. In the middle region sometimes a number of longitudinal cell rows is characterized by their narrower and longer cells. Cell walls 0.5-2 μm thick, transverse ones on average thinner than the longitudinal ones. The central thicker part of the parietal chloroplast containing the pyrenoid(s) situated often as a transverse band centrally against the peripheral cell wall, or slightly tilted towards the apically oriented anticlinal cell wall. Lobes of the chloroplast descend along the anticlinal cell walls, sometimes with a preference for the lateral ones. The chloroplast structure is seldom obscured by numerous large starch grains. 2-5 pyrenoids per cell, 1 in up to 50 % of the cells, often only 1-2 pyrenoids, 2-3 μm in diameter, round.

Anatomy, tips of short filiform branchlets (Fig. 108, 110)

In surface view, the monoseriate apex of young branchlets is 1-6 cells long. The apical cell, often also the subapical cell, are up to twice as big as the other cells. The other cells are on the whole somewhat smaller than normal thallus cells. Very young branchlets of about 6-10 cells are completely uniseriate.

Reproductive cells (Fig. 114, 116, 118)

In nature most plants are dioecious gametophytes, producing 2-flagellate gametes, the male ones slightly smaller and with smaller chloroplasts than



10µm

Fig. 126-130. – *E. flexuosa*, cells in surface view, same material as fig. 106. Fig. 126. lower basal region, lower zone. Fig. 127. lower basal region, upper zone. Fig. 128, upper basal region. Fig. 129. middle region. Fig. 130. apical region.

the female ones. They are positively phototactic and are able to germinate without fertilization. Sporophytes produce big 4-flagellate zoospores, which are also positively phototactic.

Measurements based on 22 plants (in μm)

– axis, cells in surface view :	
lower basal region, lower zone	(18-)23(-28) x (11-)13(-15)
lower basal region, upper zone	(15-)19(-22) x (9-)11(-13)
upper basal region	(15-)18(-21) x (9-)11(-13)
middle region	(11-)14(-16) x (8-) 9(-11)
apical region	(12-)14(-16) x (8-)10(-11)
– branches, cells in surface view :	
basal region	(13-)17(-20) x (10-)11(-13)
middle region	(12-)15(-18) x (9-)11(-12)
apical region	(10-)12(-14) x (8-)10(-11)
– male gametes	(5-) 6(-6.5) x (2.5)3(-3.5)
– female gametes	(6-)6.5(- 7) x (3-)3.5(-4)
– zoospores	(9-)10(-10.5) x (4.5-)5.5(-6.5)

Morphology of germlings and young fronds (Fig 107, 109)

Zoospores and fused as well as unfused gametes germinate by forming a rhizoid. This rhizoid grows very strongly, and may branch before an upright growing filament is formed. The growth of this filament is also very strong, while the rhizoidal system shows intense branching. From some spherical rhizoidal cells often more filaments are formed. At a later stage the filaments grow into hollow cylinders. The first formed frond, the main axis, may form some branches along its whole length, or predominantly on the basal part.

- Ecology and distribution

E. flexuosa has been collected from 13 stations (see Table 11 and Fig. 1).

TABLE 11. – Specimens investigated
(for locality numbers see Table 1 in KOEMAN & van den HOEK, 1982a)

1b (VII, '75, plant no. 56); 2a (VI, '75, plant no. 209); 4a (VI, '76, plants no. 552, 553, 554, 559); 5 (III, '76, plants no. 470, 471); 6b (VI, '75, plant no. 162; VI, '76, plant no. 534); 7 (V, '76, plant no. 445); 19 (IV, '76, plants no. 416, 417, 418, 419); 19a (VI, '75, plant no. 208); 22a (IV, '76, plants no. 318, 319); 25 (VIII, '76, plant no. 579); 26 (IV, '76, plants no. 360, 361); 27 (IV, '76, plant no. 427; VIII, '76, plant no. 594); 29 (IV, '76, plants no. 340, 346).

Five of these localities were low littoral sandy mudflats, where the species was growing in tidal pools. Three other localities were polyhaline man-made waters in the S.W. Netherlands. Two localities were sheltered seadikes (low littoral). Two localities were wave exposed seadikes (low littoral). Two localities were among salt marsh phanerogams on high littoral sandy mudflats, where the plants were possibly washed in from low littoral places. In one case the species was found growing in an oligohaline pond (Ameland, locality no. 4a). This distribution suggests *E. flexuosa* to be euryhaline. This was confirmed by our culture results, which gave good to very good growth at all salinities tested.

- Morphological and anatomical characters in cultures (Figs 119, 125)

The important morphological and anatomical characters were retained in cultures. The mode of branching however, was subject to wide variation. Under conditions of low salinity, fronds were broadest and sparsely branched, while in high salinity media plants were narrow, often hollow throughout the whole thallus, and densely branched. In both cases, as in wild material, some main branches were developed higher up along the axis. Cells of thalli grown under low salinity conditions contained 2-5 pyrenoids per cell, while those grown in higher salinities contained 1-2 pyrenoids per cell. The parietal chloroplast completely covered the outer cell wall, or formed a transverse band situated against the centre of the outer cell wall. At higher salinities, cells tended to be slightly smaller than in the wild material, and were generally well ordened in longitudinal and transverse rows (Table 12).

TABLE 12 (cell dimensions in µm)

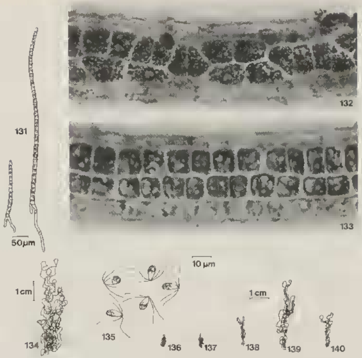
wild material of *E. flexuosa* 418	medium	in culture
upper basal region	6	(15-)23(-31) x (8-)10(-12)
(13-)18(-23) x (9-)11(-13)	5	(17-)25(-34) x (8-) 9(-10)
	4	(13-)20(-28) x (8-)10(-12)
	3	(17-)23(-30) x (9-)11(-13)
	2	(15-)21(-27) x (12-)14(-16)
	1	(17-)20(-24) x (12-)16(-20)
middle region	6	(11-)13(-15) x (7-) 9(-10)
(12-)15(-17) x (9)10(-11)	5	(11-)14(-17) x (7-) 9(-10)
	4	(14-)17(-20) x (10-)12(-14)
	3	(14-)17(-21) x (13-)14(-15)
	2	(16-)20(-23) x (11-)14(-17)
	1	(15-)18(-20) x (9-)12(-14)
apical region	6	(10-)13(-16) x (8-) 9(-10)
(14-)16(-17) x (9-)11(-14)	5	(12-)15(-18) x (8-)10(-13)
	4	(15-)18(-22) x (11-)13(-15)
	3	(15-)17(-20) x (9-)11(-12)

— ***E. RALFSII*** **Harvey**

- Description (Figs 131-140)

Morphology (Fig. 134)

Thalli filiform, curled, unbranched, narrow, with uniform diameter, light or yellowish green, forming indefinite strata or masses. Stipe absent in wild material, absolute length indefinable because of the twisted growth, but filaments of about



Figs 131-140. — *E. ralfsii*. Fig. 131. germlings, about 7 days old. Figs 132, 133. cells in surface view. Fig. 134. plant no. 270. Fig. 135. zoids from plant no. 270. Figs 136, 137, 138, 139, 140. 30 days old cultures, same material as Figs 134, Fig. 136 in 4 ‰ S medium, Fig. 137 in 9 ‰ S medium, Fig. 138 in 17 ‰ S medium, Fig. 139 in 25 ‰ S medium, Fig. 140 in 34 ‰ S medium.

50 cm length can be isolated. Width of the thalli depending on the number of cell rows (4-8), varying from 35 to 60 µm. Central cavity 8-12 µm in diameter.

Anatomy (Figs 132, 133)

In wild material no distinction could be made between basal, middle and apical regions. In parts of the thalli with low division activity, the cells are rectangular in longitudinal direction, in parts with higher division activity cells are more quadrangular, showing equal divisions. In all parts cells form longitudinal cell rows. Threads with a higher number of cell rows do not distinctly show transverse cell rows. Sometimes short 2-4 celled longitudinal cell rows are separated from each other by a thicker transverse cell wall. Cell walls 0.5-2 µm thick. The parietal chloroplast, containing the pyrenoids, completely covering the outer cell wall, or more or less contracted to a transverse band against the middle of the outer cell wall, with thin arms descending along the lateral anticlinal cell walls. The chloroplast structure is seldom obscured by starch grains. Pyrenoids 2-6 per cell, 2-4 μm in diameter, elliptic or round.

Reproductive cells (Fig. 135)

In the collected material only plants occurred which produced 4-flagellate zoids, or zoospores; the offspring of some of these plants produced 4-flagellate zoids again. They were always positively phototactic and able to germinate very soon.

Measurements, based on 5 plants (in μm)

– cells in surface view	(15-)18(-21) x (9-)11(-12)
– zoospores	(7.5)8.5(-9) x (4-)4.5(- 5)

Morphology of germlings and young filaments (Fig 131)

Zoospores germinate by forming a rhizoid, and immediately after that a strongly growing upright uniseriate filament. At a later stage these filaments grow into typical narrow cylinders, a central cavity is present when three cell rows are formed. The primary rhizoid branches at a later stage. The strongly growing filament never branches.

- Ecology and distribution

E. ralfsii has been collected from 2 stations (see Table 13 and Fig. 1).

TABLE 13. — Specimens investigated
(for locality numbers see Table 1 in KOEMAN & van den HOEK, 1982a)

6a (III, '76, plant no. 270); 7a (III, '76, plants no. 227b, 228b; V, '76, plant no. 459).

One locality was low littoral and sheltered, where the species was collected from a wooden pole; another locality was high littoral on sandy mudflats, where the species was growing in mats of *E. torta* entangled with phanerogams. Both localities are euhaline, and this seems to accord with our culture results, indicating reasonable growth at salinities ranging from 34-4 ‰ S. Other species with a euhaline distribution show the same salinity range in culture.

- Morphological and anatomical characters in cultures (Figs 136-140)

The important morphological and anatomical characters were retained in cultures. At salinities ranging from 17-34 ‰ S, the plants showed the same morphology as the original material. At 4-9 ‰ S, the filiform plants were very short and strongly twisted, which was caused by the abnormal expansion of some vegetative cells. Only at the lowest salinities tested, cells contained 3-6 pyrenoids. At the higher salinities tested, most cells contained 1-3 pyrenoids. The parietal chloroplasts were often contracted as a transverse band against the outer cell wall. Plants cultured in low salinity media had less uniform cell dimensions, and cells were on average larger than those grown in high salinity media (Table 14).

TABLE 14 (cell dimensions in μm)

wild material of *E. ralfsii* 270	medium	in culture
(20-)23(-27) x (15-)17(-18)	7	(11-)12(-14) x (6-) 8(-10)
	6	(13-)14(-16) x (7-) 9(-12)
	5	(16-)18(-20) x (8-)11(-13)
	4	(19-)21(-22) x (11-)15(-18)
	3	(17-)19(-22) x (11-)14(-17)

SECTION *CLATHRATAE* NOV. SECT.

Type species of the section *Clathratae* is *E. clathrata* (Roth) Greville, (cf. BLIDING, 1963, p. 107). The section *Clathratae* agrees with BLIDING's (1963, p. 106) «*Clathrata* Group». Only one species of this section was found along the Netherlands coast in the present study. However, STEGENGA & MOL (1983, p. 46) mention a second species of this section for the Netherlands coast, namely *E. ramulosa* (Sm.) Hook (without specifying the exact localities).

Cells in basal regions varying from about 23 x 18 to 42 x 27 μm. Cells in middle region varying from about 19 x 12 to 25 x 19 μm. Cells in apical and middle region showing mainly equal divisions, and being arranged in longitudinal rows, sometimes disturbed by unordered cell groups in broad parts of the thalli. The thin parietal chloroplast containing the 2-9 pyrenoids mostly covering only a part of the peripheral cell wall, with rather thin lobes tilted towards their common cell wall. Thallus filiform to linear, the broader thalli oblong in outline, compressed, or tubular. Plants seldom unbranched or, more usually, with main branches (having the form of the axis) and branchlets concentrated towards the basal region or along the whole axis.

Latin diagnosis

Cellulae regionis basalis magnitudine c. 23 x 18 usque ad 42 x 27 μm, cellulae regionis medianae magnitudine c. *19 x 12 usque ad 25 x 19 μm. Regionis apicalis et medianae cellulae divisionibus plerumque aequalibus in seriebus longitudinalibus (interdum in gregibus parvis irregularibus). Chloroplastus tenuis plerumque integumentum cellulare externum partim tegens 2-9 pyrenoidibus. Thallus filiformis - linearis - oblongus, complanatus sive tubulosus, rarissime simplex, plerumque ramis forma axium et ramulis praecipue in axis regione basali seu extendentibus secus axes totas.*

— ***E. CLATHRATA*** **(Roth) Greville**

- Description (Figs 141-154)

Morphology (Figs 141, 144, 146)

Thalli strapshaped to filiform, the two layers compressed, in broad parts loosely adnate with hollow margins, or completely hollow, seldom inflated. Fronds smooth, with mostly lubricous texture, yellowish green to light green,

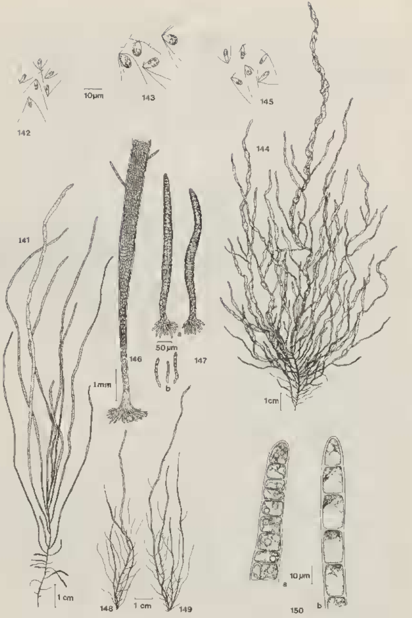


Fig. 141-150. *E. clathrata*. Fig. 141. plant no. 592. Fig. 142, male gametes. Fig. 145. female gametes. Fig. 143. zoospores. Fig. 144. sporophyte, plant no. 581, with zoospores (Fig. 143). Fig. 146. basis, same material as Fig. 141. Fig. 147. germlings, a after 15 days, b after 5 days. Fig. 148, 149. 30 days old cultures, same material as Fig 141, Fig. 148 in 17 ‰ S medium, Fig. 149 in 25 ‰ S medium. Fig. 150 tips of branchlets, showing a short celled (a) and a long celled (b) monoseriate apex, same material as Fig. 141.

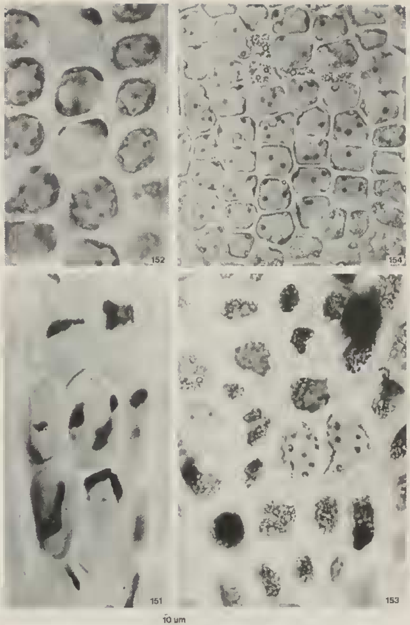


Fig. 151-154. — *E. clathrata*, cells in surface view, same material as Fig. 141. Fig. 151. lower basal region, lower zone. Fig. 152. lower basal region, upper zone. Fig. 153. upper basal region. Fig. 154. middle to apical region.

branched. Plants with branches mainly concentrated in the basal region of the thallus, or with branches along the whole main axis. Densely branched plants often with second order branches in the basal region of the main first order branches. Axis gradually narrowed towards the base into a fragile stipe, with a small disciform holdfast, from which new thalli may arise. Apices of axis and main branches obtuse. Axis and main branches up to 45 cm high and 1 cm broad, but mostly not more than 20 cm long and 3 mm broad.

Anatomy, lower basal region (Figs 146, 151, 152)

In surface view, the pale coloured stipe shows very large rhizoidal and vegetative cells, which have the same morphology. Because of their large size only a few longitudinal cell rows occur in this zone. Cells are more or less irregularly polygonal with 5-6 rounded corners, mostly elongate when not dividing. Rhizoids usually grow through the central cavity, but may also grow along the outer side of the stipe. Cell walls 1-4 μm thick. The whole chloroplast mostly covering only a part of the outer cell wall, or totally tilted towards any anticlinal cell wall. Arms relatively thin, descending along some of the anticlinal cell walls. The chloroplasts are often filled with numerous large and small starch grains, and contain 5-9 elliptic pyrenoids, 3-4 μm in diameter.

Anatomy, upper basal region (Fig. 153)

Cells in the upper basal region rounded or irregularly polygonal, sometimes predominantly rectangular with rounded corners, showing equal divisions, arranged in pairs or larger groups of cells which form undulating longitudinal rows. Often these rows are separated from each other by thicker cell walls. Cell walls 1-4 μm thick. The whole chloroplast mostly covering not more than a part of the outer cell wall. In just divided pairs of cells, the chloroplasts are often tilted away from their common cell wall. The few arms thin, descending along some of the anticlinal cell walls. The chloroplasts are often filled with numerous large and small starch grains, and contain 3-7 elliptic pyrenoids, 1-3 μm in diameter.

Anatomy, middle and apical region (Fig 154)

Cells in the middle and apical region rectangular, quadrangular or irregularly polygonal with or without rounded corners, showing mainly equal divisions, arranged in longitudinal rows, especially in the narrower branches. Sometimes this order is disturbed by groups of cells which show less order, mostly in the broader parts of the thalli. Cell walls 1-4 μm thick. The chloroplast, when covering the outer cell wall, very thin, with delicate arms descending along some anticlinal cell walls. In just divided pairs of cells, the chloroplasts are often contracted and tilted away from their common cell wall. The chloroplast structure is seldom obscured by numerous small and large starch grains. 2-6 pyrenoids per cell, 1-3 μm in diameter, elliptic.

Anatomy, tips of short filiform branchlets (Fig. 150)

In surface view, the monoseriate apex of young branchlets is mostly more than 5 cells long. The tip cell is usually slightly bigger than the other cells.

Sometimes the entire monoseriate apex consists of narrow strongly elongate cells. The other cells are on the whole somewhat smaller than normal thallus cells. Very young branchlets of about 6-10 cells are completely uniseriate.

Reproductive cells (Fig. 142, 143, 145)

In nature plants are dioecious gametophytes, producing 2-flagellate gametes, the male ones are slightly smaller and with smaller chloroplasts than the female ones, or sporophytes which produce big 4-flagellate zoospores. They appeared to be positively phototactic and were able to germinate very soon, except at temperatures lower than 12 °C.

Measurements based on 11 plants (in μm)

– axis, cells in surface view :	
lower basal region	(30-)36(-42) x (18-)23(-27)
lower basal region, upper zone	(23-)29(-35) x (18-) 21(-24)
upper basal region	(20-)25(-29) x (14-)16(-19)
middle region	(19-)22(-25) x (12-)16(-19)
apical region	(18-)21(-25) x (12-)15(-18)
– branches, cells in surface view :	
basal region	(14-)19(-23) x (10-)13(-15)
middle region	(16-)19(-23) x (-12)14(-16)
apical region	(12-)14(-16) x (7-) 8(-10)
– male gametes	(6-)6.5(-7) x (2.5) 3(-3.5)
– female gametes	(7-)7.5(-8.5) x (2.5-)3.5(-4)
– zoospores	(9-)11(-12) x (5.5-) 7(- 8)

Morphology of germlings and young fronds (Fig. 147)

Zoospores and gametes germinate by forming a rhizoid. This rhizoid grows very strongly, and may branch before an upright growing filament is formed. The growth of this filament is also very strong, while the rhizoidal system shows intense branching. From some spherical rhizoidal cells often more filaments are formed. At a later stage the filaments grow into hollow cylinders. The first formed frond, the main axis, may form some branches along its whole length, or predominantly on the basal part.

- Ecology and distribution

E. clathrata has been collected from 4 stations (see Table 15 and Fig. 1).

TABLE 15. – Specimens investigated
(for locality numbers see Table 1 in KOEMAN & van den HOEK, 1982a)

17 (VIII, '76, plants no. 572, 573, 574, 575, 576); 19 (VIII, '76, plants no. 581, 582, 583); 21 (VIII, '76, plants no. 591, 592); 27 (VIII, '76, plants no. 597, 598).

All these localities are in the S.W. Netherlands, where the species was found growing, in late summer, in the polyhaline man-made lakes. It was never found in other places. This suggests a preference for higher temperatures in summer.

In our cultures the species failed to grow at temperatures below 12°C, which accords with the distribution of the species. It behaved as an euryhaline species which gave good growth at salinities ranging from 34-1.5 ‰ S.

- Morphological and anatomical characters in culture (Figs 148, 149)

The important morphological and anatomical characters were retained in cultures. Under optimal conditions, cultured plants were coloured and branched like plants from nature. At salinities of best growth, plants had the characteristic arrangement of cells with up to 9 pyrenoids per cell. The chloroplasts of just divided cell pairs were often tilted away from each other, except in the youngest proliferations where the chloroplast was situated centrally against the outer cell wall. On the whole cells were smaller than those of the corresponding zones in the wild material (Table 16).

TABLE 16 (cell dimensions in μm)

wild material of *E. clathrata* 592	medium	in culture
upper basal region	7	(12-)16(-20) x (9-)11(-13)
(20-)24(-30) x (13-)15(-18)	6	(17-)22(-28) x (10-)11(-14)
	5	(17-)20(-22) x (14-)16(-18)
	4	(26-)29(-33) x (11-)13(-15)
	3	(22-)29(-35) x (16-)17(-19)
	2	(18-)21(-24) x (14-)15(-16)
middle region	7	(11-)12(-14) x (7-) 9(-10)
(17-)19(-21) x (13-)15(-18)	6	(9-)11(-14) x (6-) 8(- 9)
	5	(10-)12(-15) x (6-) 8(-10)
	4	(13-)15(-17) x (9-)11(-13)
	3	(20-)21(-23) x (14)16(-19)
	2	(15-)17(-19) x (10-)13(-15)
apical region	6	(13)16(-19) x (10-)12(-15)
(15-)20(-25) x (13-)15(-17)	5	(9-)13(-15) x (6-) 8(-10)
	4	(10-)14(-18) x (8-)10(-11)
	3	(18-)23(-28) x (16-)17(-18)
	2	(16-)18(-21) x (11-)13(-14)

DISCUSSION

The six taxa described in this study and found in the Netherlands, were also recognized by BLIDING (1963), namely *E. linza*, *E. linziformis* (as *E. flexuosa* ssp. *linziformis*), *E. pilifera* (as *E. flexuosa* ssp. *pilifera*), *E. flexuosa* (as *E. flexuosa* ssp. *flexuosa*), *E. ralfsii* and *E. clathrata*. However, BLIDING ranged *E. linza* in his «Linza Group» and not in his «Prolifera Group», and *E. ralfsii* in his «Torta Group» and not in his «Flexuosa Group». We range *E. linza* in the section *Proliferae*, which largely coincides with BLIDING's «Prolifera Group», and *E. ralfsii* in the section *Flexuosae*, which largely coincides with BLIDING's «Flexuosa Group», on the basis of their microscopic characters. BLIDING's «Clathrata Group» coincides with our section *Clathratae*, which was kept apart from the related section *Flexuosae*, on the basis of its microscopic characters (its larger cells; greater number of pyrenoids per cell; and its thin chloroplasts covering only a part of the outer cell wall). Five more entities placed by BLIDING in his «Flexuosa Group» were not found along the Netherlands coast, namely *E. flexuosa* ssp. *paradoxa* (incl. var. *profunda*), *E. flexuosa* ssp. *biflagellata*, *E. hendayensis*, *E. stipitata* var. *linzoides* and *E. kylinii*. Three species placed by BLIDING in his «Clathrata Group» were also absent in the collected material, namely : *E. aragoensis*, *E. multiramosa* and *E. ramulosa*.

In contrast to BLIDING (1963) we think that his three entities *E. flexuosa* ssp. *flexuosa*, *E. flexuosa* ssp. *linziformis* and *E. flexuosa* ssp. *pilifera* should be considered as three separate species mainly on the basis of macroscopic differences. Two arguments favour in our opinion the distinction of the three entities as separate species. In the first place these entities occur in the field as well recognizable populations in many different stations. In the second place the main characters are retained in unialgal cultures. The species in the section *Flexuosae* differ primarily from one another by their macroscopic morphology. This is also true for the sections *Enteromorpha* (KOEMAN & van den HOEK, 1982a) and *Proliferae* (KOEMAN & van den HOEK, 1982b). The sections however, differ from one another mainly by microscopic anatomical characters. The main characters of the section *Flexuosae* are the regular arrangement of the cells in longitudinal rows, the chloroplast with mostly 2 or more pyrenoids and thin descending lobes along the anticlinal cell walls. The main characters of the section *Proliferae* are the regular arrangement of the cells in longitudinal rows, the usual central position of the chloroplast against the peripheral cell wall and the presence of mostly one pyrenoid per cell. On the basis of these characters *E. linza* has been included in the section *Proliferae*. The four sections of *Enteromorpha* distinguished in the Netherlands can be identified with the following key :

Key to the sections of ***Enteromorpha*** occurring in the Netherlands.

1a Pyrenoids mostly one per cell (in more than 80 % of the cells) in the middle and apical region of the main frond. 2

b Pyrenoids mostly more than 2 per cell (in 50 % or more of the cells) in the middle and apical regions of the main frond 3

2a Cells in apical and middle region unordered or arranged in groups with short curved, sometimes longitudinal cell rows. The central thicker part of the parietal chloroplast usually strongly tilted towards the apical cell side, having a cap-like appearance in surface view. section *Enteromorpha*

b Cells in apical and middle region arranged in longitudinal and often transverse cell rows, or in 4-8 celled groups. The central thicker part of the parietal chloroplast usually situated centrally against the peripheral cell wall section *Proliferae*

3a Cells in the lower basal regions mostly less than 25 x 20 μm in size. Cells in apical and middle region mostly containing 2-5 pyrenoids. 1 pyrenoid in up to 50 % of the cells; chloroplasts in apical and middle region mostly

covering (almost) entirely the peripheral cell wall (if not tilted).
section *Flexuosae*

b Cells in the lower basal regions mostly more than 25 x 20 µm in size. Cells in apical and middle regions containing 2-9 pyrenoids; chloroplasts in apical and middle region thin, mostly covering only partly the peripheral cell wall section *Clathratae*

Three of the four species of the section *Flexuosae*, namely *E. linziformis*, *E. pilifera* and *E. flexuosa*, have wide ecological amplitudes with regard to salinity and prefer sheltered locations. They occur in the lower littoral zones of sandy mudflats. *E. linziformis* extends into the polyhaline man-made lakes in the S.W. Netherlands. *E. pilifera* was predominantly found in meso- to oligohaline stagnant waters, while *E. flexuosa* was found in all types of localities, even in two cases on low littoral wave exposed slopes of seadikes and harbour moles. *E. ralfsii* has a much narrower ecological range, and is limited to sheltered intertidal sandy mudflats, where it grows among salt marsh phanerogams, in mats together with *E. torta*. In culture reasonable to good growth is obtained for all species between 34-9 ‰ S. *E. flexuosa* and *E. pilifera* grew equally well at all salinities tested.

E. linza is restricted to marine environments, where it grows on wave exposed to sheltered lower littoral slopes of seadikes and harbour moles, in tidal pools and on lower littoral sandy mudflats, attached to stones, shells and other algae like *Fucus vesiculosus*. Its occurrence in the polyhaline man-made lakes in the S. W. Netherlands is remarkable because it is here represented by the type which reproduces by 2-flagellate asexual zoospores. In culture this type gave good growth at salinities between 34-4 ‰ S, whilst cultures of the open coast form, (which mainly reproduces by 4- flagellate asexual zoospores), only gave good growth at salinities between 75-25 ‰ S.

E. clathrata occurs only in the polyhaline man-made lakes in the S.W. Netherlands in late summer. It failed to grow in culture at temperatures below 12 °C. It behaved as an euryhaline species, growing well, in cultures, at salinities ranging from 34-1.5 ‰ S.

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